Seasonal changes in diets of coastal and riverine mink: the role of spawning Pacific salmon

M. Ben-David, T.A. Hanley, D.R. Klein, and D.M. Schell

Abstract: Feeding niches of riverine and coastal mink (*Mustela vison*) in southeast Alaska differ in prey composition and abundance and diving medium during spring and summer. In autumn, however, the upstream migration of spawning Pacific salmon (*Oncorhynchus* sp.) creates a pulse of food for mink. We hypothesized that diets of coastal and riverine mink, and therefore their stable isotope ratios ($\delta^{13}C$, $\delta^{15}N$), would differ significantly during periods when salmon were absent, but that salmon carcasses would constitute a large portion of the diet of both groups during the salmon spawning season. Stable isotope analyses of clotted blood cells from 24 live-captured mink and muscle tissue from 25 mink carcasses were used to indicate the composition of diets of individual mink in 1992 and 1993. These isotope values were then compared with stable isotope ratios of prey, using a multiple-source mixing model. Our results indicate that riverine mink depended on salmon (carcasses and fry), with little seasonal or individual variation, whereas coastal mink relied on intertidal organisms in spring and summer, with measurable (<25%) consumption of salmon carcasses when they became available in autumn. Coastal and riverine mink in southeast Alaska differ strongly in their diets in spring and summer, with both groups relying on the abundant salmon carcasses during autumn.

Résumé : Les niches alimentaires respectives des Visons d'Amérique (*Mustela vison*) des rivières et de la côte, dans le sud-est de l'Alaska, diffèrent par la composition et l'abondance des proies et par le milieu de plongée au printemps et en été. En automne, cependant, la migration anadrome des saumons du Pacifique (*Oncorhynchus* sp.) vers les frayères donne lieu à une période de profusion de nourriture pour les visons. Nous avons posé en hypothèse que les régimes alimentaires des visons des deux milieux, et par conséquent leurs rapports d'isotopes stables ($\delta^{13}C$, $\delta^{15}N$), doivent différer significativement au cours des périodes où les saumons sont absents, mais que les carcasses de saumons risquent de constituer une grande proportion du régime alimentaire chez les deux groupes pendant la fraye du saumon. Des analyses des isotopes stables dans des cellules sanguines coagulées de 24 visons capturés vivants et dans les tissus musculaires de 25 carcasses de visons ont servi à déterminer le régime alimentaire d'individus en particulier en 1992 et 1993. Les mesures des isotopes ont ensuite été comparées aux rapports des isotopes stables chez les proies au moyen d'un modèle de mixage de plusieurs sources. Nos résultats indiquent que les visons qui habitent les rivières consomment du saumon (carcasses et alevins) selon une variation saisonnière et individuelle très faible, alors que les visons de la côte doivent se nourrir d'organismes intercotidaux au printemps et à l'automne et comptent sur les carcasses de saumon pour une partie de leur alimentation (<25%) lorsqu'elles sont présentes en abondance à l'automne. Les visons de la côte et ceux des rivières ont donc une alimentation très différente au printemps et à l'été dans le sud-est de l'Alaska, mais les visons des deux milieux consomment des carcasses de saumon en abondance à l'automne.
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Introduction

Previous investigators described two groups of mink (*Mustela vison*) in the Pacific Northwest of North America: those

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living along the coast and those inhabiting inland riparian habitats (Harbo 1958; Hatler 1976; Johnson 1985). Although mink forage under water and hunt while diving, the relatively small surface area of their feet, their anterior propulsion, and their low oxygen storage capacity make them inefficient swimmers compared with other diving mammals (Dunstone and O'Connor 1979a, 1979b; Stephenson et al. 1988; Williams 1983, 1989; Williams and Kooyman 1985). These limitations on swimming and diving efficiency affect the duration and depth of dives, especially in seawater, which has a higher density and viscosity than fresh water (Vogel 1981). Although diving in riverine environments poses less difficulty than diving in coastal environments, the intertidal zone in southeast Alaska offers a high availability of prey species and prey biomass to foraging mink (Feder and Jewett 1986; Johnson 1985; O'Clair and Zimmerman 1986; Rogers et al. 1986). Many prey species occur in shallow waters and are slow moving (Feder and Jewett 1986; Johnson 1985; O'Clair and Zimmerman 1986; Rogers et al. 1986). Additionally, intertidal beaches and shallow rockpools provide

extensive feeding sites for mink during low tides (Ben-David et al. 1996; Hatler 1976; Johnson 1985). In comparison, the rivers in southeast Alaska are fast flowing throughout the year, and prey in them are limited to few species of fast-moving fish, mostly juvenile salmonids (Bryant 1984; Crone and Bond 1976; Murphy et al. 1988). Therefore, the feeding niches of riverine and coastal mink in southeast Alaska differ substantially.

From late summer through autumn, spawning Pacific salmon (*Oncorhynchus* sp.) carry marine-derived nutrients into lakes and rivers along the Pacific Northwest and subsequently fertilize these systems through decomposition and consumption by predators (Cederholm et al. 1989; Kline et al. 1989, 1993; Piorkowski 1995; Richey et al. 1975). Several studies in Idaho (Melquist et al. 1981) and on the Olympic Peninsula, Washington (Cederholm et al. 1989), indicated that during the spawning season mink relied on salmon carcasses for food. Therefore, the arrival of salmon in streams in southeast Alaska creates a food pulse for mink living in riparian environments.

Although investigators agreed on the importance of intertidal organisms in the diets of coastal mink, their opinions differed as to the use of salmon by these mustelids (Harbo 1958; Hatler 1976; Johnson 1985). Harbo (1958) suggested that coastal mink move upstream during the spawning season to take advantage of this resource.

We investigated seasonal changes in diets of individual mink on Chichagof Island, southeast Alaska, U.S.A., using analysis of stable isotope ratios (δ^{13}C, δ^{15}N). Analysis of food webs using the natural abundance of stable isotope ratios compares the δ^{13}C and δ^{15}N values of predator and prey tissues (DeNiro and Epstein 1981; Schoninger and DeNiro 1984; Ambrose and DeNiro 1986; Schell et al. 1988; Ehleringer and Rundel 1988; Fry and Sherr 1988; Tieszen and Button 1988; Gearing 1991; Hobson 1991; Hobson and Montevecchi 1991). Given the different foraging constraints encountered by mink in coastal and riverine environments, we hypothesized that their diets, and therefore stable isotope ratios, would differ significantly during periods in which salmon were absent. We also hypothesized that both coastal and riverine mink consume salmon carcasses to a large extent during the spawning season, therefore their stable isotope ratios will not differ significantly at that time.

Methods

Study area
The study area was located on Chichagof Island (Tenakee Springs at 57°52′N, 135°18′W; Fig. 1). The region has a maritime climate; summers are cool and wet and winters are characterized by deep snow (2360 mm annual precipitation). The snow-free period extends from early May to early November at lower elevations. Vegetation at higher elevations is typified by alpine tundra and at lower elevations by coastal old-growth rain forest consisting of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) with a well-developed understory (mainly *Oplopanax horridus*, *Vaccinium* sp., *Menziesia ferruginea*, and *Rubus* sp.). The study area encompassed six streams that supported an annual run of three species of spawning Pacific salmon: pink salmon (*Oncorhynchus gorbuscha*), chum salmon (*O. keta*), and coho salmon (*O. kisutch*). Pink and chum salmon migrated upstream and spawned from early July to late September (Heard 1991; Salo 1991), whereas coho

salmon entered the streams from early September to late November (Sandercock 1991). Adult Dolly Varden (*Salvelinus malma*) and adult steelhead trout (*O. gairdnerii*) entered the streams in late May. Adult Dolly Varden remain in the streams until the end of November. Pink and chum salmon hatchlings emerged from the gravel in late March and migrated downstream to the sea by early June (Murphy et al. 1988; Ben-David 1996). Juvenile coho salmon emerged from the gravel from early May to mid-July and remained in fresh water for up to 2 years (Crone and Bond 1976; Bryant 1984, 1990; Ben-David 1996). Similarly, juvenile Dolly Varden and steelhead reared in fresh water for ≤2 years (Armstrong 1970; Ben-David 1996). Two additional fish species are common in the freshwater systems of the island: coastrange sculpin (*Cottus aleuticus*) and threespine stickleback (*Gasterosteus aculeatus*). The intertidal zone supports a large variety of intertidal fish species (such as the sculpins *Oligocottus maculosus*, *Icelinus borealis*, and *Leptocottus armatus*; the gunnel *Pholis laeta*; and others, *Stichaues punctatus*, *Bathymaster signatus*, *Lumpenus maculatus*, *Xiphister atropurpureus*, *Xiphister muscosus*, *Theragra chaleogramma*, *Ammodytes hexapterus*) and intertidal invertebrate species (such as the blue mussel, *Mytilus trossulus*; the amphipods *Anonyx* sp.; the hermit crab *Pagurus* sp.; the crabs *Telmessus cheiragonous*, *Hemiprapsus oregonensis*, *Hemiprapsus nudus*, and *Pugettia gracilis*; and the shrimps *Pandalus platyceros*, *Pandalus danae*, and *Hippolytida* sp.). Possible mammalian prey for mink on the island include Keen's deer mice (*Peromyscus keeni*; also known as *P. sitkensis* (see Hogan et al. 1993)), long-tailed voles (*Microtus longicaudas*), tundra voles (*Microtus oeconomus*), red squirrels (*Tamiasciurus hudsonicus*), and common shrews (*Sorex cinereus*).

Sampling mink
We trapped mink during three seasons: summer (late May to early August), autumn (early October to late November), and spring (mid-March to early May) in 1992 and 1993. Twenty-four adult mink (10 females and 14 males; Table 1) were live-captured repeatedly (some individuals up to 5 times per day) using Tomahawk live traps (Model 203; Tomahawk Live Trap Co., Tomahawk, Wis.) during spring and summer (Table 1). We were unable to capture more than one mink from late July to late November, although we observed mink along our traplines regularly during that period. We captured one individual female (4 times) on the coast during the last 2 weeks of November 1993. Individuals originally captured on the coast during summer 1992 and 1993 were trapped repeatedly within the same habitat, and individuals originally captured along rivers were also trapped repeatedly along rivers throughout summer (Table 1). During the mating season in spring, we captured 6 male mink that were long distances (3−7 km) from their original capture point and in both habitats (Table 1).

After immobilization with an injection of ketamine hydrochloride (15 mg/kg body mass; Aveco, Fort Dodge, Iowa), each individual was measured, weighed, and marked subcutaneously with a passive integrated transponder tag (Biosonics, Seattle, Wash.). A 2-cc blood sample was drawn from the jugular vein of each mink once a season and stored in a glass or plastic vial. Animals were released at the site of capture. Blood was spun at 3000 rpm for 5 min using a manual centrifuge within 2 h after collection, and serum was siphoned into a separate vial. Both serum and samples of clotted blood cells were frozen (−18°C) until analysis. All methods used in this study were approved by an independent Animal Care and Use Committee at the University of Alaska Fairbanks.

Additionally, 25 mink carcasses were obtained from trappers in late autumn 1992 and 1993. Date and location of capture were recorded for each carcass. We determined age, sex, body measurements, and mass of each carcass before a 5- to 10-g muscle sample was excised from the hind leg for stable isotope analysis.

Fig. 1. Location of study area (shaded) on Chichagof Island, southeast Alaska.
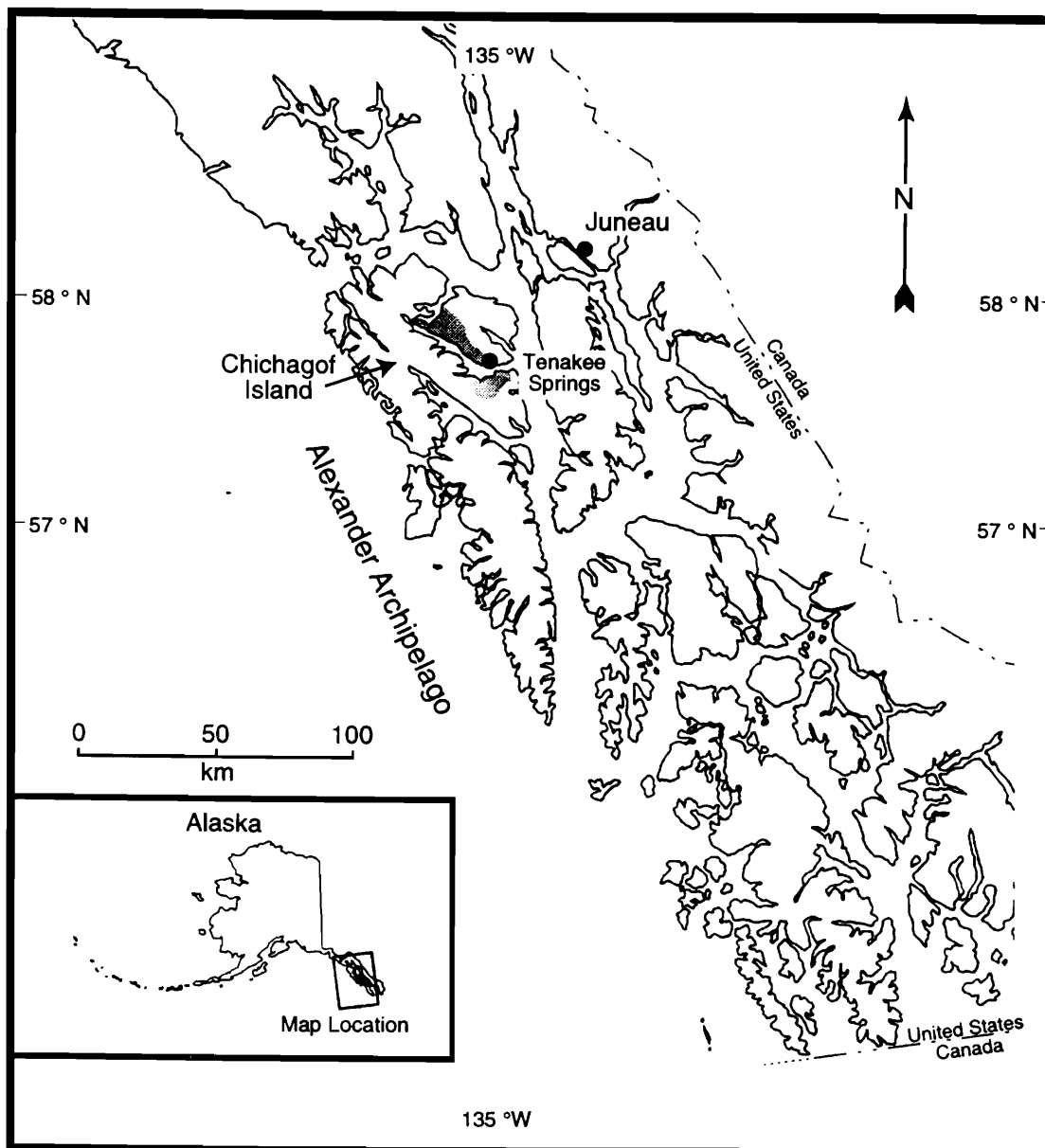
Table 1. Numbers of captures of male and female mink on Chichagof Island, southeast Alaska, during each season from summer 1992 through autumn 1993.

	Summer 1992		Autumn 1992		Spring 1993		Summer 1993		Autumn 1993	
	n	Mean ± SD	n	Mean ± SD	n	Mean ± SD	n	Mean ± SD	n	Mean ± SD
Males										
River	3	9.0±6.1		—	10	3.5±3.2	4	3.8±4.6		—
Coast		—		—	5	2.0±1.2	4	1.5±1.0		—
Females										
River	2	2.5±2.1		—		—	4	1.0±0.0		—
Coast	1	4.0		—	1	4.0	2	3.5±2.1	1	4.0

Note: Two male riverine mink were caught along the coast and 4 male coastal mink were captured along streams in spring 1993.

Sampling prey

Seven to 13 trapping grids, each containing 25 Sherman live traps in a 20 × 20 m arrangement, were set on 3 consecutive nights in all three seasons (summer, autumn, and spring). The trapping grids were set within 50 m of the stream bank or mean high tide and traps were baited with rolled oats and peanut butter. All Keen's deer mice and long-tailed voles that we live-captured were marked with paint and released; a subsample of 2 individuals per species were randomly selected from each grid and euthanized with halothane (Halocarbon, River Edge, N.J.). A muscle sample was collected from each euthanized individual for stable isotope analysis. Additional samples were obtained from rodents collected in companion studies by T.A. Hanley (U.S. Forest Service, Pacific Northwest Research Station) and R.W. Flynn (Alaska Department of Fish and Game). The remainder of each carcass was prepared as a museum specimen (including frozen tissues) and archived at the University of Alaska Museum.

Concurrently, at each trapping site, 5 minnow traps were set at 5-m intervals in the stream or along the coast below mean low tide. Minnow traps were baited with salmon eggs in the river and with bait herring in the intertidal zone. Trapped fish and marine invertebrates were identified to the level of genus or species (Trautman 1973) and counted, and a random sample of 2 individuals per species for each trap was collected for stable isotope analysis. Juvenile coho salmon were assigned an age-class (0+, 1+, 2+ years) according to their fork length (Murphy et al. 1988; Ben-David 1996). Similarly, for further analysis, other species of freshwater fish were grouped according to the same criterion (fork length).

In addition to the trapping grids, 10 transects, each 50 m long, were walked along the beach at low tide in each season. Additional samples of intertidal fish, crabs, and blue mussels (*Mytilus trossulus*) were collected from tidal pools for stable isotope analysis. Tissue samples (including muscle, skin, fat, and bones) from adult Dolly Varden and pink, chum, and coho salmon were obtained from individuals captured in dip nets or from carcasses that were encountered while monitoring traplines for mink along the streams from late May to late November 1992 and 1993. Muscle samples from mallards (*Anas platyrhynchos*), buffleheads (*Bucephala albeola*), and mergansers (*Mergus merganser*) were obtained from hunters in November.

The choice of tissues for isotope analysis was based on observations of feeding mink in the wild (M. Ben-David, personal observation), and the need to maximize use of euthanized animals as required by the Institutional Animal Care and Use Committee.

Analysis of stable isotope ratios

Tissues (clotted blood cells, muscle samples, and whole fish and invertebrates) were kept frozen between collection and preparation for determination of stable isotope ratios. Samples were dried at 60–70°C for 48 h and then ground to a fine powder using a Wig-L-Bug grinder. Samples of intertidal invertebrates were then dissolved in 95% hydrochloric acid solution to remove calcium carbonates and redried. Subsequently, a 1- to 1.5-mg subsample was weighed into a miniature tin cup (4 × 6 mm) for combustion. We used a Europa C/N continuous-flow mass spectrometer to obtain the stable isotope ratios. Each sample was analyzed in duplicate and results were accepted only if the variance between the duplicates did not exceed that of the peptone standard. We determined the diet source for each mink on the basis of the combined $\delta^{13}C$ and $\delta^{15}N$ values. We used the dual-isotope multiple-source mixing model (Kline et al. 1993; Ben-David 1996) to estimate the relative contribution of each prey item to the diet of individual mink. This model uses the mean $\delta^{13}C$ and $\delta^{15}N$ values for each type of prey (*A*, *B*, *C*, etc.) corrected for the enrichment in a predator's ratios compared with its diet (i.e., the fractionation value; DeNiro and Epstein 1981;

Tieszen and Boutton 1988; Kline et al. 1993). The Euclidean distance between the corrected isotope values of a prey item and each predator (i.e., the distance between the predator, *P*, and each corrected prey species, *A'*, *B'*, *C'*, etc.) is then calculated as $z = \sqrt{x^2 + y^2}$. The contribution of each prey item to the diet of the predator is inversely related to the distance between the corrected signature of the prey species and the predator (i.e., the shorter the distance the greater the contribution). Because of this inverse relationship, the relative contribution (%) of each prey item to the diet is calculated as

$$[1] \quad X = (PX'^{-1}/PA'^{-1} + PB'^{-1} + PC'^{-1}) \times 100$$

where *X'* is *A'*, *B'*, or *C'*.

The mixing model requires that the isotope values of all prey be significantly different from each other in bivariate space. This model assumes that each individual predator consumes all possible types of prey, therefore it will tend to overestimate the proportion of food items that are rarely consumed and underestimate the proportion of commonly used prey. Consequently, we used the model as an index of prey consumption rather than for calculating actual proportions in the diet.

For carbon we used fractionation values of 2‰ when mammalian and avian prey were consumed and 1‰ when fish or invertebrates were consumed, based on results from feeding experiments in captivity on mink and black bears (*Ursus americanus*; Ben-David 1996; Hilderbrand et al. 1996). For nitrogen we used fractionation values of 3‰ when mammalian prey, avian prey, and invertebrates were consumed and 2‰ when fish was consumed (Ben-David 1996). We introduced to the model only prey items that were captured on the trap grids and transects as well as avian prey observed in the study area, assuming that our censusing was indicative of the availability of such prey to mink. Because stable isotope values of clotted blood cells did not differ significantly from those of muscle in experiments on captive mink (Ben-David 1996), we pooled data obtained from live animals and those from carcasses in some of our analyses.

Statistical analysis

Because of small sample sizes, data from different years were pooled by season. We employed a *K* nearest-neighbor randomization test (Schilling 1986; Ben-David 1996) to investigate whether stable isotope ratios of all possible prey sampled were significantly different from each other. In this test, $\delta^{13}C$ and $\delta^{15}N$ values are treated as spatial data because the units of measurement in both variables are equal and stable. This test determines the probability that the two observed samples are derived from the same population compared with the probability that samples with the same values were generated at random. The *K* nearest-neighbor randomization test uses a Bonferroni correction when evaluating the differences between all possible prey (Ben-David 1996). We used Pearson's χ^2 test to investigate differences in abundance of prey between seasons (BMDP; Dixon 1990) and the Kruskal–Wallis test with multiple comparisons or the Mann–Whitney test (Zar 1984) to compare differences in the proportions of prey types/items in the diet of mink between seasons. Although using Kruskal–Wallis and Mann–Whitney tests with repeated samples is a form of pseudoreplication, no nonparametric tests for repeated measures are currently available.

Results

Stable isotope ratios of riverine prey

Stable isotope ratios of juvenile coho salmon did not differ significantly from those of juvenile pink and chum salmon of age 0+ in spring and summer (*K* nearest-neighbor randomization test, *P* = 0.3614; Table 2). Therefore, we termed this

Table 2. Stable isotope values of possible prey for mink in riverine and coastal environments on Chichagof Island, southeast Alaska, during 1992 and 1993.

| | Summer | | | | | Autumn | | | | | Spring | | | | |
| | | $\delta^{13}C$ | | $\delta^{15}N$ | | | $\delta^{13}C$ | | $\delta^{15}N$ | | | $\delta^{13}C$ | | $\delta^{15}N$ | |
	n	Mean	SE	Mean	SE	n	Mean	SE	Mean	SE	n	Mean	SE	Mean	SE
River															
Small fish	13	−22.19	0.4	13.61	0.66	—	—	—	—	—	24	−21.88	0.23	12.83	0.21
Large fish	124	−23.82	0.17	11.79	0.13	125	−24.27	0.22	12.13	0.25	36	−24.46	0.29	11.91	0.21
Sticklebacks	10	−29.41	0.47	9.95	0.35	10	−29.17	0.45	10.33	0.49	14	−29.48	0.62	10.04	0.32
Rodents	60	−28.4	0.21	6.76	0.15	49	−26.48	0.16	4.04	0.22	18	−26.61	0.5	7.07	0.28
Salmon	46	−20.09	0.23	12.57	0.21	18	−18.65	0.18	13.01	0.13	—	—	—	—	—
Ducks	—	—	—	—	—	6	−23.38	1.06	11.92	0.98	—	—	—	—	—
Coast															
Tidal fish	76	−16.61	0.15	11.68	0.11	16	−16.23	0.21	12.3	0.16	15	−15.23	0.22	12.68	0.09
Blue mussels	19	−19.03	0.14	7.77	0.09	15	−18.62	0.17	7.78	0.86	11	−19.51	0.26	7.74	0.15
Crabs	39	−15.41	1.08	8.07	0.14	42	−17.15	0.16	8.6	0.1	20	−16.28	0.22	9.2	0.16
Shrimps	6	−17.67	0.09	10.04	0.08	11	−17.62	0.23	9.82	0.09	6	−17.9	0.39	9.96	0.21
Amphipods	—	—	—	—	—	19	−17.13	0.25	11.5	0.4	25	−19.69	0.18	12	0.19

group small fish. Stable isotope ratios of juvenile coho salmon aged 1+ and 2+ did not differ significantly within each season (K nearest-neighbor randomization test, $P = 0.5327$ in summer; $P = 0.9443$ in autumn; $P = 0.9625$ in spring; Table 2). Similarly, there was no significant difference in the isotope ratios of coho salmon in these age groups and juvenile Dolly Varden or coastrange sculpins of the same fork lengths ($P = 0.747$). Therefore, we were unable to differentiate between species and size groups of these fish and regarded them as one diet group termed large fish.

Isotope ratios of deer mice did not differ significantly from those of voles ($P = 0.2606$; Table 2), therefore we were unable to differentiate between them and regarded them as one diet group termed small rodents. Likewise, no significant difference occurred in the stable isotope ratios of ducks and large fish in all seasons (K nearest-neighbor randomization test, $P = 0.7684$; Table 2), therefore we were unable to determine the relative contribution of ducks to the diet of riverine mink.

Our final classification of types of prey of riverine mink consisted of sticklebacks, small fish, large fish, adult salmon (including adult Dolly Varden), and small rodents (Table 2). The K nearest-neighbor randomization test revealed that all these prey types were significantly different from each other in all seasons ($P < 0.05$), except small and large fish in autumn ($P = 0.5634$). Additionally, there was a significant difference in the stable isotope ratios of small fish between summer and autumn and between spring and autumn ($P < 0.001$). Although the stable isotope ratio of small fish differed significantly from that of adult salmon (K nearest-neighbor randomization test, $P < 0.001$), the small fish in spring (mainly pink and chum; Table 2) had an isotope signature characteristic of a marine environment.

Diet of riverine mink

Stable isotope ratios obtained from riverine mink (Fig. 2) did not show significant differences among seasons (K nearest-

neighbor randomization test, $P > 0.3$). Results from the multiple-source mixing model (Table 3) indicate that summer and autumn diets of mink consisted largely of salmon. Nonetheless, because salmon carcasses are unavailable to mink in spring, this prey was not introduced to the mixing model in that season. The mixing model identified small fish as the main prey in diets of riverine mink in spring (51 ± 2.6%). The relative contribution of small fish to the diet of mink in summer and autumn was significantly lower than in spring (Table 3; Kruskal−Wallis test, $P < 0.05$).

Large fish, sticklebacks, and small rodents made a relatively small contribution to the diet (Table 3). Although the relative contribution of large fish did not differ significantly between spring and summer (Mann−Whitney test, $P < 0.05$; Table 3), their contribution to the diet in autumn could not be determined independently of that of small fish.

### Stable isotope ratios of coastal prey

Stable isotope ratios of intertidal fish of different species and sizes did not vary significantly within each season (K nearest-neighbor randomization test, $P = 0.0801$), therefore we were unable to differentiate among them and regarded them as one dietary group that we termed intertidal fish. Similarly, no significant differences were detected between the different species of crabs and hermit crabs in each of the seasons (K nearest-neighbor randomization test, $P = 0.4412$), and they were treated as a single group.

Our final selection of prey sources for coastal mink were intertidal fish, crabs, shrimps, amphipods, blue mussels, adult salmon, ducks, and small rodents (Table 2). The K nearest-neighbor randomization test revealed that all these prey types were significantly different from each other in all seasons ($P < 0.05$).

Diet of coastal mink

Stable isotope ratios of coastal mink (Fig. 2) differed significantly between summer and autumn (K nearest-neighbor ran-

Fig. 2. Values (mean ± SE) of $\delta^{13}C$ (●, ○) and $\delta^{15}N$ (▲, △) for riverine and coastal mink on Chichagof Island, southeast Alaska, in 1992–1993, plotted against season. Open symbols represent live-captured mink and closed symbols represent mink carcasses.
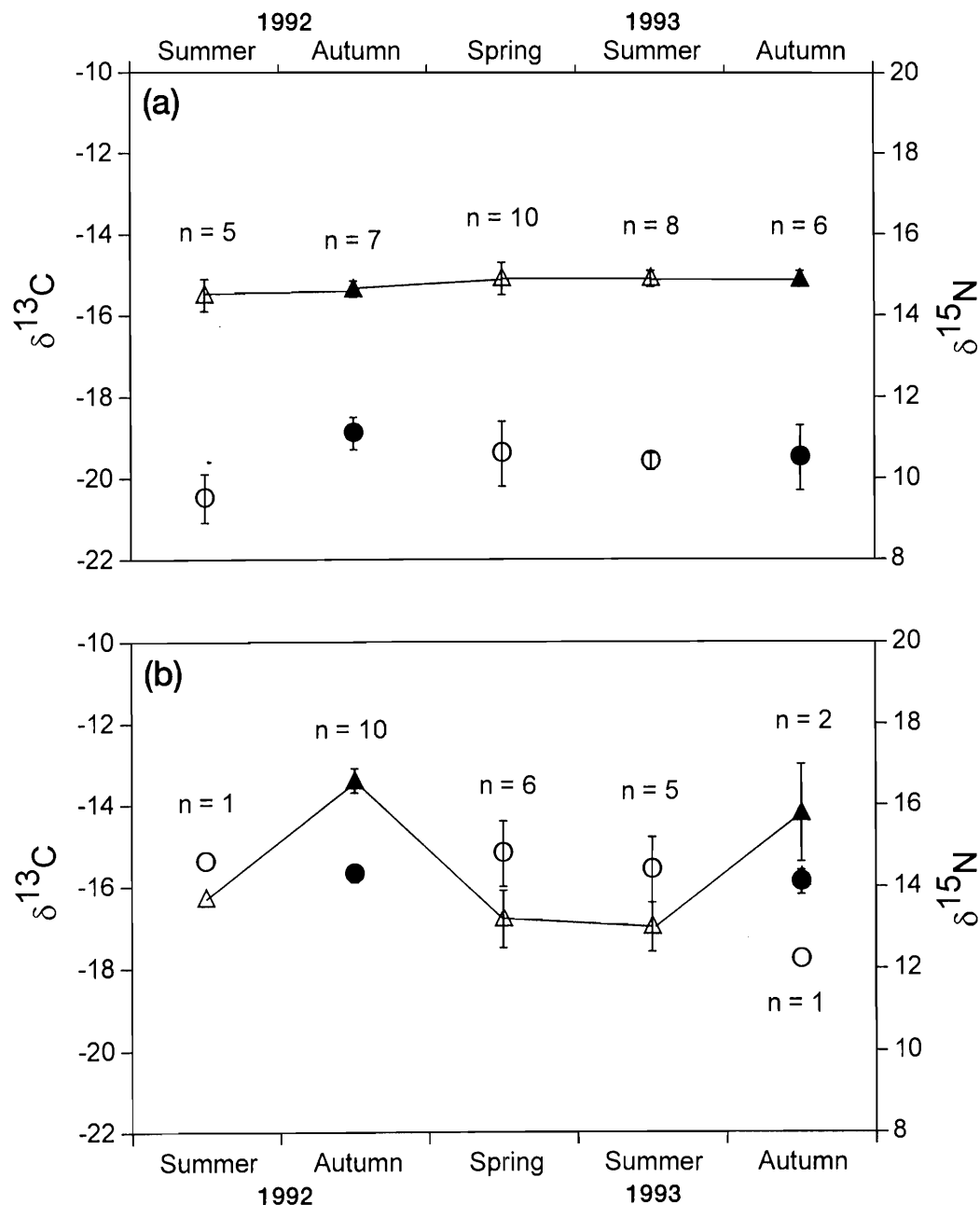
domization test, $P < 0.001$) and between spring and autumn ($P < 0.001$), but not between spring and summer (K nearest-neighbor randomization test, $P = 0.961$). Results from the multiple-source mixing model (Table 3) indicate that diets of coastal mink in spring and summer consisted largely of intertidal fish (Table 3). In autumn, the percentage of intertidal fish decreased significantly (Kruskal–Wallis test, $P < 0.05$). The relative contributions of intertidal organisms other than fish were comparatively small and did not show significant differences among seasons (Table 3), except that of crabs, which increased during spring. In autumn, several individual mink had high $\delta^{15}N$ values that could not be fully explained by the consumption of salmon or any of the other prey

species we sampled, contributing to the elevated $\delta^{15}N$ values in Fig. 2. The relative contributions of small rodents and ducks to the diet of coastal mink were small and did not change with season (Table 3).

Comparison of coastal and riverine mink

The stable isotope ratios of coastal and riverine mink differed significantly in spring and summer (K nearest-neighbor randomization test, $P < 0.001$; Fig. 2). Similarly, stable isotope ratios of coastal mink in autumn differed significantly from those of riverine mink in that season (K nearest-neighbor randomization test, $P < 0.001$; Fig. 2).

Table 3. Relative contributions (%) of prey items to the diet of coastal and riverine mink (n) captured on Chichagof Island, southeast Alaska, during 1992 and 1993.

Prey item	Summer Mean	Summer SE	Autumn Mean	Autumn SE	Spring Mean	Spring SE
Riverine mink						
n	13		13		10	
Small freshwater fish	24	1.5a	24	4.1a	51	2.6b
Large freshwater fish	17	3.5a	—		23	1.0a
Sticklebacks	5	0.3a	9	1.2b	11	0.4b
Rodents	5	0.4a	9	1.1b	15	1.2c
Salmon	49	4.6a	57	6.1a	—	
Coastal mink						
n	6		13		6	
Intertidal fish	44	9.3a	17	1.7b	30	8.3ab
Blue mussels	17	9.5a	7	0.3a	12	4.5a
Crabs	12	2.3a	9	0.4a	21	5.3b
Shrimp	18	3.0a	12	0.4a	17	2.2a
Rodents	3	0.5a	3	0.3a	5	1.4a
Amphipods	—		21	1.0a	9	0.9b
Ducks	5	0.8a	7	0.4a	6	1.3a
Salmon	—		23	3.0	—	

Note: Percentages were calculated using the multiple-source mixing model. Values followed by a different letter are significantly different between seasons at $\alpha = 0.05$ (Kruskal–Wallis test with multiple comparisons).

Discussion

Marine-derived nutrients (C and N) play a major role in the diet of riverine mink on Chichagof Island throughout the year. Mink consumed adult Dolly Varden in early summer, spawning pink, chum, and coho salmon in summer and autumn, and emerging juvenile salmonids in spring.

Although emerging juvenile salmonids are small, mink are efficient at catching small fish that occur in loose schools (Poole and Dunstone 1976). In addition, large numbers of juvenile coho salmon and Dolly Varden, mostly of age-class 0+, were commonly trapped in shallow off-channel pools following floods in our study area (up to 600 individuals per pool; M.N. Rosing, personal communication). Such off-channel pools offered little cover and left the fish highly exposed to predation by mink, otters, and mergansers (M.N. Rosing, personal commuication).

An additional contribution to the marine signature of riverine mink in spring could be consumption of salmon carcasses cached in autumn. We observed several (5) mink carrying carcasses away from the stream bank in summer and autumn, and located frozen salmon carcasses (13) in root cavities of large spruce trees as well as under rock overhangs. We were unable, however, to quantify the availability of such carcasses. Introducing salmon as a potential prey to the mixing model in spring reduced the relative contribution of small fish to the diet of mink to 32 ± 1.5%. Nonetheless, this value indicates that the role of small fish in spring diet of mink is still substantial.

The comparatively low percentage of other freshwater fish in the diet of mink is comparable to those reported in other studies on mink in North America, and in Europe,

where mink are feral (Gerell 1967; Chanin and Linn 1980; Wise et al. 1981; Dunstone 1993). Other studies, however, reported higher percentages of large freshwater fish (Melquist et al. 1981). This difference could be due to the ample cover provided for fish in the streams of southeast Alaska (Bryant 1984; 1990; Bisson et al. 1987; Sullivan et al. 1987). Dunstone and O'Connor (1979a) have shown that available cover for prey is the most important factor affecting predatory success of diving mink.

Mammals played a lesser role in the diet of mink in our study area than elsewhere (Gerell 1967; Melquist et al. 1981; Dunstone and Birks 1987; Dunstone 1993). We offer three possible explanations: (1) our study area was especially rich in marine resources; (2) populations of small rodents in our study area were at low densities in 1992 and 1993 (Ben-David 1996), and few other potential mammalian prey were available on Chichagof Island; and (3) there were differences in the techniques used in the different studies of mink diets. Gerell (1967), Chanin and Linn (1980), Melquist et al. (1981), and Dunstone and Birks (1987) used fecal or gastrointestinal analyses, which tend to overestimate the occurrence of prey items with large amounts of indigestible, readily recognizable tissues such as fur, small bones, teeth, and jaws.

When comparing the results of fecal and gastrointestinal analyses with the isotopic composition of animals tissues, it is important to note that isotope ratios are in part determined by metabolic pathways (Schwarcz 1991; Tieszen and Fagre 1993). Therefore, if a consumer assimilates structural lipids and proteins from one source but derives most of its energy from another source, the latter will be underestimated when the consumer tissues are analyzed (Schwarcz 1991). Similarly, Hobson et al. (1993) demonstrated that $\delta^{15}N$ enrichment occurs when animals are nutritionally stressed and therefore the $\delta^{15}N$ value alone might not closely reflect the diet. In addition, because of the assumptions associated with the mixing model, caution should be exercised when comparing our results with those of other studies.

Unfortunately, we were unable to determine the relative contribution of ducks to the diet of riverine mink because we could not isotopically differentiate them from large freshwater fish. Avian prey usually constitute a small portion of mink diets (Gerell 1967; Chanin and Linn 1980; Melquist et al. 1981; Wise et al. 1981; Dunstone 1993), although waterfowl may be important when locally abundant (Eberhardt and Sargeant 1977). Ducks were not especially abundant in our study area, and evaluation of the relative contribution of ducks to the diets of coastal mink demonstrated that the contribution of this prey was comparatively small.

Diets of coastal mink in our study area comprised largely intertidal fish in summer and spring, which is consistent with results of other studies of the feeding ecology of coastal mink (Hatler 1976; Cuthbert 1979; Johnson 1985; Dunstone and Birks 1987). The combined percentages of invertebrates constituted the other major portion of the diet. Our analysis indicates, however, that crabs did not constitute a large portion of the diet of mink, contradicting reports from most other populations of coastal mink. On the other hand, shrimps and amphipods formed a greater portion of the diets of mink than has been reported elsewhere (Hatler 1976; Cuthbert 1979; Johnson 1985; Dunstone and Birks 1987). The discrepancy

could be a result of differences in techniques used or between study areas, or both.

Diets of coastal mink included a measurable (<25%) amount of salmon carcasses when they became available in autumn. Johnson (1985) reported similar results for mink on Prince of Wales Island, southeast Alaska. Coastal mink could obtain salmon carcasses in estuaries; however, Cederholm et al. (1989) reported that less than 4% of salmon carcasses are washed from rivers to estuaries. Therefore, coastal mink would have to move upstream to search for this resource. Johnson (1985) did not observe such movements among his radio-tracked mink, and our mark−recapture records (Table 1) indicated strong fidelity to habitat. Nonetheless, we had great difficulty trapping mink in autumn (presumably because of the high abundance of salmon), and our data provide no additional insight into movements of mink in that season. We did, however, capture male mink long distances (3−7 km) from their original capture site and in both habitats in spring. Although these movements were most likely associated with breeding rather than feeding, they suggest that mink are capable of moving long distances in search of important food resources.

In conclusion, the stable isotope ratios suggest that coastal and riverine mink in southeast Alaska occupy two different feeding niches in spring and summer. This observation raises questions concerning specialization in foraging strategies, fidelity to a feeding niche by the foraging mink, population genetics, and early-age imprinting on food by mink. In autumn, the two groups of mink rely on the abundant salmon carcasses. This significant seasonal pulse of resources is likely to determine several aspects of mink ecology in southeast Alaska, such as timing of reproduction (Ben-David 1997) and dispersal patterns, and merits further investigation.

Acknowledgments

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